VI.—*Some remarks on the development of Pollen. By* William Griffith, *Assistant Surgeon, Madras Establishment.*

Pollen of *Pardanthus Chinensis*, Ker. Nat. Order *Irideæ*.

At the earliest period submitted to examination, and when the perianth scarcely exceeds half a line in length, the anthers are sessile and nearly perfectly formed. The cells, of which (as is perhaps the case in all bilocular anthers) there are four, contain a solid grumous semi-opaque mass, which is easily detached from the cell by slight pressure. This mass under a lens whose focal distance is one-twentieth of an inch, shews evident traces of cellularity, but the outlines of the cells are very faint. They are entirely filled with exceedingly minute granular matter. At a somewhat later period the cellularity of the mass is more obvious, but no separation of the component parts has taken place, and the cells are still entirely occupied by the granular matter.

When the perianth has attained the length of a line and a half, the mass will be found to have become externally of an orange colour, and traces of a proper enclosing membrane, the cells of which are extremely indistinctly marked, are now visible. The membrane appears to have no connection with the interior of the loculus. The cells composing the mass have undergone some separation. They consist of a hyaline membrane which appears to be of some thickness; it is generally of a globular form, but often attenuate at one or both ends. The granular molecular matter which originally filled the whole cavity of the cell, now occupies a portion only, and never appears to lose its spherical form. When the perianth is two lines long, the proper membrane of the mass has become more distinct; its cells contain a good deal of granular matter of a reddish orange colour. The cells of the mass have become more separated, but have otherwise undergone no change; the semi-opaque nucleus presents traces of division most frequently into four, often into three, and very rarely into two portions. The division is more distinct towards the circumference of each cell; it may be observed in the same mass in every stage, from the commencement of the dividing lines to their meeting in the centre. The smaller masses or nucelli resulting from this division are each enclosed in a proper cell, but as yet have undergone no separation.

In the next stage the perianth had increased two-thirds of a line in length; the mass presented externally the same appearance. The component cells had increased in size, and the divisions of the nucleus had in many cases undergone complete separation from each other,

and in all were separable by slight pressure. Each of these divisions is at this period a young grain of Pollen. On making their escape they leave their proper cells attached to the interior of the parent cell, which is hence divided into as many cells as there are divisions of the nucleus. The young grains are oblong-ovate, flattened on their contiguous or inner faces, and open along the centre throughout the whole length of their outer faces. They are even at this period reticulate, and have rather a papillose appearance; they are lined by an inner membrane in the form of a hyaline sac which bulges out slightly along the opening just mentioned.

When the perianth is three lines long, the grains of Pollen have undergone complete separation; no traces of their original envelopes being visible. They vary much in size, are rather opaque, minutely reticulate, and marked along one side by a longitudinal semi-transparent line, which indicates the situation of the original opening, now closed up by the inflection of its edges. Immersion in water produces scarcely any action on them. At a later period, the perianth measuring five lines in length, the grains are considerably increased in size. Immersion in water causes the inflected margins of the furrow to secede, until they become widely separate. Through this the inner membrane bulges out to a considerable extent.

Perianth about six lines in length: the Pollen is now perfectly formed; the grains vary much in size, the smaller being probably abortive, but theya ll undergo the same changes on immersion in water. This causes the outer coat to be pushed back by the expansion of the inner, which is now nearly filled with minute granular matter.

At the time of dehiscence of the anthers the grains vary much in size: the more perfect are lanceolate in outline, of an orange colour, distinctly reticulate or cellular, and open on one side along the centre. This, however, is perhaps to be attributed to the excessive moisture of the climate. Immersion in water causes the very rapid bulging out of the inner membrane, which pushes back, and at length nearly entirely off, the outer one. This is filled with minute granular matter, the fovilla and burst of the immersion is somewhat protracted.

Stigmatic action causes the production of a tube or boyau from the inner membrane, the head of which tube continues to be covered partially by the outer coat.

This instance is interesting as an example of the development of Pollen by the division of an originally simple nucleus and of perfect and almost spontaneous separation of the outer coat, and lastly as

pointing out clearly the nature of the longitudinal furrows of such common occurrence in the ordinary forms of Pollen.

In the two other instances which I have selected as demonstrations, the steps are much the same. Care must be taken not to confound the appearance presented by the Pollen of *Luffa fœtida* at a late period of its development, and which evidently arises from the strong inflection of the outer membrane, with that occasioned by the much earlier dividing process.

In *Hedychium* I have been unable to examine the development at a sufficiently early period, but it appears to me the divisions of the original or parent cell form the outer coats of the subsequent grains of Pollen: this is certainly not usually the case. The Pollen of this plant is remarkably simple, for it is neither provided with furrows nor apparent pores.

The inner coat,—for I am disposed to believe that it has one,—adheres strongly to the outer, and none of the ordinary means are sufficient to ensure its separation.

As I have, since a portion of the above was written, received numbers of the Annales des Sciences Naturelles for March and April 1835, in which occur extracts of considerable length from the writings of Mr. Hugo Mohl, who has published lately (1834) at full length on this important organ, it may not be amiss here to state the principal results to which this botanist has arrived; noticing, however, only those which relate to development and structure.

After pointing out that in by far the greater number of cases, the inner membrane, which contains the fovilla, is enclosed in a second membrane, M. Mohl proceeds to a detailed account of the outer membrane. This is represented as being always finer than the inner, and as generally determining the form of the grain; and that it is to the liquid secreted by it that the colour and viscosity of the grain is to be attributed.

The punctuation which frequently exist in this membrane are supposed to be rudimentary cellules; hence the comparison of this coat to a simple cellule is altogether inexact; it should be considered as an organ composed of cellules or the rudiment of cellules, and a homogeneous uniting membrane, and hence it should be compared with compound membranes; such, for instance, as those of the ovule.

It is only in a small number of plants that this coat presents the form of a perfectly closed, continuous, sphærical sac; in most cases it is either furnished with folds or pores, or both.

Up to the period of M. Mohl's publication nothing whatever was known of the nature, functions, or number of these folds; most bo-

tanists, so far at least as may be judged of from their descriptions, considering them to be solitary. M. Mohl remarks, that in monocotyledones they are generally single, but that in dicotyledones the number is generally increased, and occasionally exceeds twenty. The portion that is folded in has always a different structure from the remainder, and is generally smooth and transparent; and it rarely ever happens that in cellular Pollen the inflected portion is itself cellular. He supposes that in all cases the outer membrane forms a perfectly closed sac, although in some Pollen the inflected portion has more of a gelatinous than a membranous consistence, and is ruptured by immersion in water. The apparent pores visible in the Pollen of many plants, M. Mohl states to be in all cases covered over by a thin membrane—to the existence of this membrane over the larger pores he speaks positively. In those cases in which the membrane covering the pore separates in the form of an operculum, it is attenuated alone along the margin of function or continuation with the remainder of the outer coat. These statements accord with the author's views of the nature of the supposed pores of cellular tissue; views, however, which have not been generally received, and which in the case of cellular tissue are open to weighty objections. The inner membrane is represented as always having the same structure; it is always completely homogeneous, very thin, and hyaline, and always exists as a shut sac. It is particularly remarkable for the facility with which it absorbs water; this M. Mohl looks upon as a physical action and as attributable to endosmosis.

The production of tubes (boyaux) by immersion in water, (and which are prolongations in all cases, except perhaps in *Coniferæ*, of the immediate covering of the fovilla) never takes place in those Pollens, the outer membrane of which is perfectly closed, or the folds or furrows of which are unprovided with pores. But in every Pollen they are produced by stigmatic action. The action likewise exerted on the grains by this portion of the female organ is more energetic than that of water, producing twelve or fifteen times the diameter of the grain; while the longest, M. Mohl observed, produced by the action of water only exceeded the grain in length once, or once and a half.

I may here state, that M. Mohl has understated the length of the tubes arising from stigmatic action. The length will depend upon the distance between the part of the stigma to which the grains are applied and the foramen of the ovulum to which they have to be applied. Thus, for example, in Zea mays, the length of the tubes must be enormous, since the style itself is about a span long. It may be

objected, that there is no proof of the universal necessity of the application of the tube to the foramen, or that portion of the ovulum corresponding to this. Still there is ample proof of this necessity in Asclepiadeæ; and, as I have observed it in *Solaneæ*, *Gentianeæ*, *Nelumboreæ*, and *Leguminosæ*, I have no doubt that the application of the tube to the foramen is absolutely necessary to insure fecundation. And with regard to the length produced by the action of water, I have seen tubes produced from the grains of Pollen in a species of *Impatiens*, I believe the *Impatiens tripetata* of Roxburgh, exceeding six or eight times the long diameter of the grain; these tubes, however, never even after protracted immersion contained any granules. Their growth in the above instance may be actually watched, the apex of the tube creeping along with an excessively slow vermicular motion.

M. Mohl states, that *Asclepiadeæ* alone have no outer membrane. The existence of this membrane as a distinct integument has been proved by Mr. Brown; although in almost all the species of this family, the outer coats are in a state of mutual adhesion*.

Coniferæ are said to have three coats; the intermediate one resembling the inner membrane of ordinary Pollen, especially in its great extensibility; in this property the innermost, although it has the ordinary structure of inner membranes of other Pollens, is deficient.

As I have mentioned before, this author considers the outer membrane as the secretory one, and he denies the possession of secretory powers by the papillæ; an opinion stated to be advanced by Mr. Brown. M. Mohl proves that the secretion of oil is not limited to any papillosity of surface; of this *Pardanthus Chinensis* is an instance.

This botanist doubts the proper activity of the molecules or granules contained in the fovilla, and he adduces the authority of M. Fraunhofer as to the utter impossibility of preventing currents in liquids.

* I find that the cells of the anther of *Oxystelma esculentum* are at an extremely early period lined by a free *simple* sac containing irregular masses of opaque granular matter; soon after, this cell appears to be filled entirely with the granular matter, by which it is rendered somewhat turgid. In this state it is detachable with extreme difficulty. When the flower bud is two lines long, the mass has become cellular, and the granular matter correspondingly subdivided. The subsequent changes consist merely in the increase of size and consistency of the parts, and perhaps in the development of the inner membrane. We may hence be allowed to infer that the mass, from which all Pollen grains seem to be developed, is in *Asclepiadeæ* reduced to a single cell: and that the grains are produced by its indefinite division. The only material objection to this view exists in the original cell itself entering into the composition of the grains of Pollen; and in its not disappearing, as appears to be generally the case.

Still I conceive it impossible to doubt the inherent mobility of these granules. In some oily Pollens granules may be observed by the sides of excessively minute drops of oil, certainly not exceeding the larger granules twice in diameter; and yet the granules will be seen in active motion, and the oil perfectly stationary. M. Mohl contradicts positively the curious fact advanced by M. Adolphe Brongniart, that the granules are in some plants of the same size. Of this I certainly have never met with an instance. He likewise doubts the curvature of some molecules; but as Mr. Brown and M. Brongniart speak positively on this point, I should prefer adopting their testimony.

It is, likewise, said, that the idea of the granules nourishing the tubes is untenable, and founded only on conjectures. But as it invariably happens that the longer the tube is the fewer the granules are, this opinion, which was I believe first indicated by the highest of all authorities, Mr. Brown, cannot be said to be destitute of foundation.

With regard to the development of Pollen, M. Mohl states that his observations entirely confirm those of M. Brongniart, and that the Pollen is formed from the granular matter contained in the cells of the parenchymatous mass, which exists in each cell of the anther. But although M. Brongniart certainly appears to have been the first to have observed the formation of pollen by division, yet his account in his "Memoire sur la generation et le developpement de l'embryon dans les vegetaux phanerogames," is certainly not characterised by that precision which exists in the account of the development of the Pollen in *Tradescantia virginica* by Mr. Brown, and subsequently in that of *Cucurbita Pepo* by M. Mirbel.

This latter, indeed, was the first instance examined by M. Brongniart, who states that what are now known to be lines of division result from pressure. It still remains to be proved whether in any instance the formation takes place, as M. Brongniart says it does, in *Cucurbita Pepo*, by the cellules of the mass contained in the cavities of the anthers becoming directly grains of pollen. M. Mohl mentions many instances in which the quaternary division is resorted to; it is owing to the continuance of the original adhesion that the pollen of many plants is compound. The number, however, is not in every case thus limited: the generality of the species of *Mimosa*, *Acacia*, *Inga*, have pollen composed of sixteen cellules. But on the development of these no direct observations have as yet been given. The number of masses into which the originally simple nucleus may be divided, is almost as frequently three as four. Of the binary composition of the mature Pollen *Podostemon* affords the only instance as

yet known to me, but this may obviously arise as well from a quaternary as a binary division of the nucleus.

M. Mohl rejects very properly as highly improbable the opinion of M. Brongniart, that the granules of the fovilla are secreted by some part of the inner surface of the cells of the anther, and that they reach their destination, the cavity of the inner membrane of each grain, by absorption. It must, however, be remembered that M. Brongniart alludes to this mode of formation and transmission with considerable doubt.

Lastly, M. Mohl notices the extreme similarity between the formation of the pollen and that of the sporules of the more developed *Cryptogamia*. I am not aware who first pointed out this curious analogy, which cannot well have escaped any one who has examined both formations at a sufficiently early period. My first knowledge of it is due to M. Mirbel, who pointed it out to me early in 1832*.

Explanation of the figures, Plate XLI.

1. Portion of a mass extracted from a loculus; perianth 1 line in length.
2. Ditto ditto; perianth $1\frac{1}{2}$ line in length.
3. Three of the component cells of a mass; perianth $1\frac{2}{3}$ line long.
4. Four similar cells more developed; perianth about 2 lines long.
5. Portion of a mass enveloped in its membrane, extracted from the cell of an anther; perianth 2 lines in length.

5*a*. Two of the component cells detached.

6. Four of the cells detached: (perianth $2\frac{2}{3}$ lines long:) viewed in different aspects:—from one, three nuclei have escaped, and the fourth is half exserted.

* *Equisetaceæ* do not, as might be supposed from their late elevation into an order of *Gymnospermæ*, differ from the higher forms of *Cryptogamia* in the development of their sporula. The spiral fibres, as might be expected, are of comparatively late appearance, and they are developed on or in a loose membranous coat, no traces of which are to be found until the sporula have assumed their proper form. The fibres subsequently, and about the time of the development of the fibres of the cells of the inner parietes of the capsules, become free, the membrane to which they were attached remaining as an envelope to the sporule, from which it subsequently becomes separable with facility. The granules are of still later appearance.

To the correctness of the chief portions of the above statement I can speak with tolerable confidence, but I only infer that the hyaline envelope of the perfect sporule is the mature state of the tunic, to which the spiral fibres are originally attached.

There would hence appear to be no foundation whatever for the adoption of the idea of the sexuality of *Equisetaceæ*,—an idea very likely to meet with advocates from its extreme ingenuity. The analogy of the fibres or supposed filaments is to be looked for in the elaters, and of the tunic or envelope in the tunic of the sporules of many *Hepaticæ*.